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THE OCCURRENCE OF AMITOSIS IN MONIEZIA.

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In a recent paper, "On the Method of Cell Division in *Tænia*," by A. Richards,¹ the author records his failure to find amitotic division in *Tænia* and suggests on the basis of his results that my conclusions concerning amitosis in *Moniezia*² are due to errors of observation.

The appearance of this paper makes it necessary for me, in defence of my observations, to emphasize certain features of my own work, to which Richards has apparently not given adequate consideration, to add a few observations not included or only briefly referred to in my earlier papers and finally to subject his attempts at interpretation to critical analysis.

In the first place, it might seem that the reading of my statement concerning methods of fixation and precautions employed (I., pp. 89-93) would suggest to anyone that I had exercised at least some degree of care in order to avoid errors of observation of so gross a nature as the mistaking of a mass of "Nebendotter" for a nucleus. As I stated, fresh material was fixed by the most various methods during each of four successive years, and a large part of my time during this period was devoted to the study of the preparations, from which hundreds of camera drawings were made. The work was begun simply because the apparent absence of mitosis in certain regions of growth interested me, and I expected to find either some unusual type of mitosis or else short recurrent periods of mitosis. What I did find, however, led me to exercise the utmost care and to go over the ground repeatedly even after I had published my preliminary paper in 1904.³ During the whole period of my work I was constantly searching for

¹ BIOL. BULL., XVII., 4, 1909.

² Child, "Studies on the Relation between Amitosis and Mitosis," I., BIOL. BULL., XII., 2, 1907; II., *ibid.*, 3-4; III., *ibid.*, XIII., 3, 1907; IV. and V., *ibid.*, 4. In later references to these papers in the text they will be designated simply by the Roman numerals I.-V.

³ "Amitosis in *Moniezia*," *Anat. Anz.*, XXV., 22, 1904.

modified forms of mitosis as a possible basis for interpretation, but the frequency and almost diagrammatic clearness of the cases which I could interpret only as direct division, satisfied me that no such interpretation was possible. I have pointed out (I., pp. 91-2) the difficulties attendant upon the observation of amitosis in fixed material and the methods employed for giving the greatest possible certainty. Cases of apparent division which appeared in the slightest degree doubtful were not accepted as evidence. I have demonstrated many cases of apparent amitosis to others, both students and colleagues, who were able to see them with perfect clearness and had no doubt of their being what they seemed to be.

On pp. 312-313 of his paper Richards says: "I must protest against the balancing of results obtained from such unfavorable material as that which cestodes offer against such favorable objects for cytological study as for example the Orthoptera." This protest involves somewhat peculiar ideas of cytological study. Apparently, according to Richards, we must draw our conclusions from "favorable" material and leave the unfavorable aside. And apparently also because certain phenomena are clearly visible in favorable material, *e. g.*, the Orthoptera, we must conclude that the phenomena in other less favorable material are essentially similar. No field of biological science, and perhaps no field of science in general, has suffered to such an extent as has morphology from premature generalizations based on observation of one or a few forms. Indeed it is perhaps not too much to say that limited observation and premature attempts at generalization often go hand in hand.

As regards the "unfavorable" character of the *Moniezia* tissues I must disagree to some extent with Richards. With proper fixation, with sections sufficiently thin—most of mine were 2-3 micra—and with careful staining and extraction, the material is no more difficult to study, at least as regards nuclear phenomena, than many other tissues. I have seen hundreds of cases of apparent amitosis which were almost diagrammatic in their clearness when observed with a little care, though of course not as conspicuous as certain phenomena of mitosis in certain species and cells. If observation of fixed and stained material is

of any value at all as a means of discovering the visible phenomena of cell division, I can only conclude that direct division occurs in *Moniezia* as I have stated and that it can be seen readily enough by anyone who is willing to take sufficient care in preparation and observation.

Moreover, I have not, so far as I am aware, attempted at any time to "balance" my observations against those of others. The real point at issue is not my observations against those of others, but my observations against a hypothesis, which cannot be proved by observation, viz., the chromosome hypothesis, for the only real objection to the acceptance of my observations at their face value is the existence of this hypothesis. I do not wish to enter into fruitless discussion of the hypothesis, but merely to emphasize the fact that I have attempted in every way possible to make the record of my observations a record of actual fact. Such records cannot be controverted either by observations on another genus and species or by invoking a hypothesis which is far from being proved. It is interesting to note that Richards' paper is to a considerable extent devoted to "balancing" his observations against my own, although both according to him are made on the "unfavorable" cestode material.

Turning now to certain matters of detail, we may consider first certain points with respect to the parenchyma. My observations on amitosis began with a study of the neck-region, *i. e.*, the region between the scolex and the first visible proglottids. In this region the tissue of the body consists mainly of parenchymal cells, muscle fibers, the nerve cords and the nephridial canals. At the posterior end of this region the proglottids become visibly marked off one after the other, each including a certain portion of the tissue. In other words, the cells which constitute each proglottid either preëxist, or arise by the division of preëxisting cells in the neck-region, or else they must arise *de novo*. Examination of transverse sections at short intervals from the scolex backward into the proglottid region shows a very considerable increase in the number of nuclei, as I have determined by actual counts of the nuclei in the sections. In short there can be no doubt that new parenchymal nuclei are formed in this region, and when we consider the enormous number of proglottids formed

from a single neck-region and observe that the number of nuclei in the neck-region at any given time is sufficient for only a few proglottids it becomes evident that during the life of the animal an enormous number of new nuclei is formed in some way in this region. These facts dispose of Richards' conclusion that the parenchyma grows chiefly by the formation of "intercellular material."

Moreover, in view of these facts it is not in the least surprising that Richards has failed to observe any division, either mitotic or amitotic in the parenchymal cells (p. 323), since, so far as can be determined from his statements, he has apparently paid little or no attention to the neck-region. Mere observation of the method of growth and the abundance of nuclei in this region forces us to conclude, either that nuclear divisions occur in enormous numbers in this region or else that nuclei are formed *de novo*, an alternative which most of us would hesitate to accept without proof of the most conclusive character.

When one examines scores of these neck-regions, as I have done, and finds first absolutely no mitoses and second hundreds of cases of apparent amitosis, many of them almost diagrammatic, the evidence for the occurrence of amitosis acquires at least some value.

On p. 322 Richards says: "Child has assumed all through his work that the absence of mitotic figures in tissues known to be growing rapidly is evidence of the occurrence of division by amitosis." He then proceeds to show that the growth of the parenchyma occurs to a large extent by the formation of "intercellular material." This statement of Richards seems, so far as it concerns my own position, to be an error. My argument is actually as follows: When mitosis is absent from regions where rapid increase in the number of nuclei is manifestly taking place, we have good reason to believe that some other form of nuclear division is occurring, especially when we have discovered what appears to be this other form in other tissues of the same animal.

I have, I think, made it sufficiently clear all through my work that in speaking of regions of rapid growth I meant not merely regions in which the cells were increasing in size or forming intercellular material but those in which they were actually increas-

ing in number. I have never, however, considered absence of mitosis in such cases as proof of the occurrence of amitosis. Only the actual observation of amitosis can prove that it is occurring.

I wish to add to my earlier observations the fact that in a single individual consisting of scolex, neck-region and a few of the youngest proglottids, I have found almost every nucleus in mitotic division. This is the only case of the sort which I have ever observed. Aside from this I have never seen a single case of mitosis in this region of the body. I am inclined to believe that this is a young animal in the early stages of growth. In my work on various other forms, as yet unpublished, I have found considerable evidence in support of the view that amitosis becomes more frequent as growth (with cell division) becomes more rapid. In *Planaria*, for example, regeneration begins with mitosis, but as the growth of the new tissue becomes more rapid amitosis takes the place of mitosis. Patterson¹ has found that the frequency of apparent amitosis increases in regions of rapid growth, and other evidence to be presented elsewhere exists.

For those to whom the positive observations on amitosis are of little or no value as evidence this case of mitosis in the neck-region of *Moniezia* opens a way for simple interpretation. They will conclude, as Richards suggests (p. 320), that mitosis is of short duration and occurs in waves, *i. e.*, is periodic, and that all the other individuals observed by me are simply stages between two such periods. At present, however, I cannot accept such an interpretation as the correct one. Not only the cells of the neck-region, but the cells of the scolex, which does not take part in the growth of other regions are undergoing mitosis in this specimen. Moreover, I am as yet unable to convince myself that the many cases of apparent amitosis, which I have observed, in the neck-region of other individuals, are all errors of observation, or something else than nuclear division.

Concerning the structure of the nuclei in *Moniezia*, it may be said merely that the non-chromatic portions of the "embryonic nuclei" present widely different appearances with different fixing agents. After Hermann's fluid the nuclear structure of the primitive germ nuclei and the parenchyma nuclei is somewhat similar

¹ "Amitosis in the Pigeon's Egg," *Anat. Anz.*, XXXII.; 5, 1908.

to that figured by Richards for *Tænia*, but after comparing the results of various fixing agents I came to regard it as highly probable that the "strands of linin" were simply coagulation products and therefore stated (I., p. 93) that "a distinct reticular structure does not appear." Richards (p. 316) attributes to me the statement that "the nuclei do not contain any definite reticulum." Though I am not desirous of splitting hairs this seems to me a much more positive statement than that which I did make. I do not know how widely different the nuclei of *Moniezia* are from those of *Tænia*, and while I could give figures showing "strands of linin" in some of these nuclei, I am strongly skeptical, for the reasons given above, as to their representing in *Moniezia* a real nuclear structure existing before fixation. As the germ cells approach maturation the visible nuclear structure undergoes alteration, as my figures show, and the non-chromatic portions show more definite and constant characteristics. Richards in his work has apparently employed only Flemming's and Zenker's fluids, both of which will, under certain conditions, produce reticular structure in solutions of proteids. Since the "strands of linin" were sometimes confusing in the study of the nuclear membrane I often found it desirable to extract the stain to such an extent that they were only slightly stained, or to employ fixing agents which did not show them in the resting nuclei.

But the chief interest centers of course about the occurrence or non-occurrence of amitosis in the germ cycle. It is evident that if all the nuclei which are included in a given proglottid arise, or may under certain conditions arise, in the neck-region by amitotic division the germ cells must arise from nuclei which have previously divided amitotically. This conclusion is, however, open to the objection that since we cannot be certain that every individual nucleus in the neck-region has divided amitotically, it may be possible that the nuclei of the germ cycle have not so divided. This objection is actually of little force, for there are probably not enough parenchymal nuclei in the neck-region at any one time to give rise even to all the mother germ cells which appear. Nevertheless this objection must be reckoned with and I should not for a moment maintain that the amitotic division in the neck-region constitutes absolute proof of the occurrence of amitosis in the germ cycle.

In my own work I proceeded posteriorly from the neck through the youngest proglottids to the region in which the reproductive organs first appear, and then followed their development from this point to and through the process of maturation. In the primitive germ cells mitosis is more or less frequent, as I have shown in my earlier papers, and if I had not found the most positive evidence of the occurrence of amitosis I should not have doubted that in this period cell division was wholly mitotic. But I found it is impossible to convince myself that this was the case, simply because I observed too frequently what I could not interpret as anything but amitosis.

Richards has not found amitosis in the germ cells, but he does not state what stages in the development of the reproductive organs he has examined. If one may judge from his figures and his statement on p. 313 that "the female sex cells in the cestodes in question are by far the largest cells in the body," it would appear that he has examined only the later stages, in which the cells have already assumed the definite characteristics of germ cells. In these stages I myself have never been able to observe amitosis with certainty, though mitosis is often seen.

It is during what one might designate as the embryonic development of the reproductive organs, when the germ cells, at least in the female, are not visibly different, from the cells which form the vitellaria and the reproductive ducts, that I have found amitosis, though even in these stages mitosis sometimes occurs. In order to forestall a possible objection, I should perhaps call attention again to the fact already noted in my earlier work (I., pp. 97-109) that after certain stages the portions which are to form the ovary can readily be distinguished from those which are to form vitellaria and ducts by their position and method of growth, though the cells are all still apparently similar.

Richards says absolutely nothing concerning these earlier stages in his work on *Tenia*, and until further evidence is forthcoming, it seems at least possible that his failure to discover amitosis may have been due to the fact that he examined only stages where it does not occur. However, I know nothing from personal observation as to the occurrence or non-occurrence of amitosis in the species which Richards has examined, and since

I am inclined to believe that the relative frequency of mitosis and amitosis in certain species, and even in single individuals, *e. g.*, *Planaria* may vary greatly according to conditions, it is also possible that Richards' material differs more or less widely from mine.

And now a few words concerning Richards' attempts at interpretation of my observations on the germ cells. On p. 315 he suggests that I have been misled by mistaking for a nucleus or part of a nucleus a mass of "Nebendotter" which occurs in "some of the early oögonia . . . while it is not present in some oöcytes" (p. 313). That one investigator working with one species should be willing, without more positive evidence than Richards has anywhere brought forward, to attribute to another, of wider experience than himself, and working with a different species and genus, so gross an error of observation as this is, to say the least, somewhat surprising. But the facts are these: as I have noted above, amitosis occurs in the earlier stages of development of the ovary and in such stages the primitive germ cells certainly contain no "Nebendotter." As a matter of fact, I have never seen anything of the sort at any stage in the ova of *Moniezia*, although the cells of the vitellaria, which in certain stages may easily be mistaken for ova, develop such masses rather early in their history, but usually not until division has ceased (see Child, I., Figs. 31-35, and pp. 112-3). I cannot see that my accounts of nuclear structure and division afford any possible basis for the relief that I could have mistaken for a nucleus a body which according to Richards stains readily with iron hæmatoxylin and appears "as a dark homogeneous mass even after a great deal of extraction," by which "nucleus and cytoplasm may be entirely decolorized" (Richards, p. 314). Moreover I have employed various methods of staining which leave the yolk almost wholly unstained.

Concerning the slight difference in color between the two parts of a nucleus, which I noted occasionally (Child, I., p. 95), it need only be said that I have often observed such differences in the somatic cells of *Moniezia*, as well as in the somatic cells of other forms, where there can be no question concerning "Nebendotter," consequently Richards' suggestion (p. 315) that

one of the parts in such cases is "Nebendotter" falls to the ground.

As regards Richards' interpretation of "endogenous" division (Child, I., p. 95), which he presents in connection with the case of mitosis shown in his Figs. 17 and 18, it may be said that such attempts at interpretation of another's observations are scarcely worthy of criticism. The statement of an author that he has employed so far as possible every precaution and has repeated his observations again and again to avoid error, is ordinarily given some degree of consideration. Moreover, as regards this particular point I stated (Child, I., pp. 95-6) that "some cases of this sort of almost diagrammatic clearness have been observed." And finally reference to a few figures (*e. g.*, I., Fig. 13*E*; II., Figs. 9*A* and 9*C*) is sufficient to show that the parts in such divisions are often very different in size and the membranes perfectly distinct throughout. There is then not the slightest basis for regarding them as misinterpreted mitoses.

To sum up: Richards' evidence for the non-occurrence of amitosis is wholly negative, my evidence for its occurrence is positive. How far his failure to find amitosis may be due to failure to examine the proper stages and how far to the actual absence of such phenomena as I have described, it is impossible to determine. Second, his attempts at interpretation of my results as errors of observation are wholly unsuccessful, since they concern stages of development very different from those on which I have based my conclusions and occurring in another genus, and since they involve a total disregard of much that I have said concerning methods, precautions, the appearance of the nuclei, etc.

The whole question of the occurrence or non-occurrence of amitosis is one which requires great care and extended research, and it may be doubted whether it is a suitable subject for a beginner in cytological investigation, both because of his lack of experience and because he is likely to be guided to a greater or less extent by the views of his instructor.

I wish to add a brief remark concerning my later observations on amitosis in other forms.¹ In this paper I merely recorded the

¹Child, "Amitosis as a Factor in Normal and Regulatory Growth," *Anat. Anz.*, XXX., 11 and 12, 1907.

occurrence of what seemed to me to be undoubted cases of amitosis in a number of species from different groups of the animal kingdom, without attempting in most cases to determine its frequency or significance, and added a brief consideration of the physiological and theoretical significance of amitosis in general. Concerning my observations in this paper Richards says (p. 311) that my "evidence is lacking in some respects." I scarcely see how other evidence than positive statements and figures can be given and must suggest the desirability of more definite criticism than this, for in discrediting another's observations it is no more than just to present definite reasons for one's position.

And finally : if my observations are not in accord with certain current hypotheses it is not because of any preconceived opinions on my part concerning those hypotheses, but simply because the results of my work have forced me to believe that the hypotheses are not in accord with all the facts. As regards this point, it would seem that our present knowledge of regulatory phenomena in organisms is sufficient to show very clearly that certain results may be attained in different ways under different conditions. Moreover, the periodical recurrence of specific structures in definite form and number is one of the most characteristic features of the organic cycle, but we do not regard it as necessary to believe that those structures should persist as distinct and continuous entities during the periods when they are not visible. To speak specifically, why should we regard the chromosome problem as fundamentally different from the problem involved in the recurrence in each generation of five fingers upon a hand, or the regulatory development of a definite and characteristic number of tentacles in a piece of an actinian body ? The farther we proceed in our physiological analysis of developmental phenomena, the more evident does it become that the finger and the tentacle do not persist as distinct and definite entities during all the period when they are not present as visible structures. The only thing which persists is the physiological capacity to react in a certain way under certain conditions, and when these conditions arise the characteristic structure-complex appears.

In short, when we consider the chromosome problem from a physiological instead of a purely morphological point of view, and

we must consider it in this way sooner or later, we can find no good reason for regarding it as fundamentally different from many other problems of ontogeny. Physiologically it is no more difficult to conceive that a piece of a nucleus should, under certain conditions, give rise to the characteristic number of chromosomes, than that a piece of the actinian body should give rise to the characteristic number of tentacles. The correctness of the chromosome hypothesis is far from being demonstrated, and in view of this fact we must consider the possibility of revising the hypothesis to fit the facts, as well as that of bringing the facts into accord with the hypothesis.

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